The Annual Activity of Intermediary Roots of the Aleppo Pine

BY
B. LESHEM

Abstract. A study was made of the annual activity of intermediary roots of *Pinus halepensis* Mill. Roots were uncovered monthly around a few marked trees at three different groves, situated on different soils at varying heights above sea level. In the dormant root tip, metacutization was found to conform to type II of Plaut (1909). The suberized layer surrounds the initials and their immediate derivatives and unites by a bridge of suberized cells in the cortex with the secondary endodermis. When growth is resumed the cortical bridge persists and is seen as a brown band across the cortex, while the remnants of the layer which surrounds the apex are pushed to the outer boundary of the newly formed cortex. The main root activity takes place in the rainy winter and ceases in the dry summer. A pronounced resumption of root growth was observed in late summer, even though there was no rainfall. This growth ceased, and then was resumed at the onset of the winter rains. Neither a complete rest in root growth nor general activity was shown. Phenological observations show a lack of correlation between root and shoot growth. Inducing root growth by edaphic as well as other factors is discussed.

THE TERM "Heterorhyzy" was applied to woody plants by Hartig (1878), Von Alten (1909), and Noelle (1910) for description of the root system from the functional point of view. They distinguished between long roots "Langwurzeln" which were to fulfill the task of anchoring the plant and extending its root system, and the short roots "Kurzwurzeln" which served for absorption of water and nutrients. Noelle (1910) described, in the incense cedar, the short roots as diarch and roots with 3, 4, or 5 protoxylem positions as true long roots. Aldrich-Blake (1930) defined in the Corsican pine short "mother roots" as diarch and long "pioneer roots" as triarch. Nevertheless he admitted that short mother roots can eventually be converted into long pioneer roots while growing.

Such distinction, does not include, by definition the mass of lateral roots of higher orders which make up the main volume of the root system. These roots can possess 2, 3, or 4 protoxylem positions and yet be short. They can, as well, burst into a rush of growth and become long roots which extend the root system. These roots can develop secondary bodies, thus changing into thickened roots with anchoring functions. Long roots can fulfil the task of absorption at their distal portions. Thus, any definition of roots

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according to function or anatomical features is arbitrary and of doubtful value. Earlier work of Flaskämper (1910) and recent works of Wilcox (1962) and Ginzburg (1964) also prove the need of regarding the root system as a continuum without functional specialization and lacking distinction on the ground of anatomical or morphological characters.

In our survey we investigated roots 1–10 cm long with diameters from 0.4–0.7 mm, which did not develop any secondary tissues. For the purpose of description in the present work we shall call them intermediary roots.

The anatomical structure of the dormant root tip was first described by Müller (1906). He used the term "Metakutisierung" to describe the process of suberization following lignification occurring in certain cells of the cortex and the dormant root cap. Wilcox (1954) adopted the term "metacutization", which is a translation of the German word. Müller (1906) found that, in a large variety of monocotyledoneous plants, the apical meristems appeared to be isolated from the calyptra and primary cortex by the "metacutis". Plaut (1909) studied the dormant roots of Gymnosperms, and found four distinct types of metacutization in that group.

In the present study a description is given of the activity of the intermediary roots of Aleppo pine (*Pinus halepensis* Mill.) throughout the yearly cycle. Aleppo pine was selected because it is the most prevalent conifer planted in the forests of Israel. We hoped to find in the root tips the metacutized layer which accompanies dormancy and was described for other conifers. Special attention was given to the influence of edaphic conditions, which alternate in Israel from a cool rainy winter to a hot dry summer, on the formation of this corky layer.

Materials and Methods

The sites selected for studies on root activity were groves and forests of Aleppo pine situated at Rehovot, on deep red sandy soil, 50 m above sea level; in the "Panorama" forest of the J.N.F.[1], on light grey calcareous rendzina; about 300 m above sea level; and in the Neve Ilan J.N.F. forest in the Judean mountains, on heavy red soil (terra rossa), poor in limestone, about 700 m above sea level. The trees varied from 9 (Neve Ilan) to 20 (Rehovot) years old.

The eastern Mediterranean region is characterized by a rainy winter and an entirely dry summer. In this area, soil in the upper layers dries far below the wilting point and tree roots are exposed to high water stress.

Table 1 shows the rainfall measured at meteorological stations near or at the experimental localities during the 1962–63 season, which was an exceptionally dry one. Except at Rehovot, there was hardly any rain in January, most unusual for this month.

Once every month, from Dec. 1962 until Nov. 1963, roots were excavated at a depth of 25–30 cm from different places around a few marked trees. At this depth also soil temperature was measured on soil thermometers which were installed at the beginning of the year. Soil water content was determined from samples taken monthly at the places of root excavation at the three selected sites. Preliminary phenological observations were made, mainly on the lower branches which in spring bear many male inflorescences.

Sampling roots at 25–30 cm depth is reasonable under the conditions of this region, since it is the main root horizon of intermediary roots. This layer is relatively rich in nutrients and keeps water more than superficial soil layers. The first 15 cm of the soil are too dry and hot in summer to harbor any roots.

Distal portions of intermediary roots 0.5 to 3.0cm in length were collected monthly from the excavated roots. They were bleached in NaCl O for 10 min. following

[1] Jewish National Fund.

TABLE 1. Total monthly rainfall during the 1962/63 season at meteorological stations near the sites of root sampling (mm)[1].

Month	Locality			
	Rehovot	Eshtaol NE of Panorama	Tsora S of Panorama	Beit Meir S of Neve Ilan
Oct. 1962	22.6	5.0	4.9	12.1
Nov.	--	--	--	--
Dec.	120.8	83.0	56.9	85.8
Jan. 1963	101.3	14.0	15.4	18.2
Feb.	51.4	93.0	57.2	107.1
Mar.	18.1	27.5	25.0	35.3
Apr.	16.4	23.5	27.7	22 3
May	1.8	8.0	4.8	6.5
June	--	--	--	--
July	--	--	--	--
Aug.	--	--	--	--
Sept.	--	--	--	--
Oct.	44.4	41.0	33.5	42.4
Nov.	86.3	84.0	72.0	68.6
Dec.	196.6	229.5	220.1	268.4

[1] Data supplied by the Israel Meteorological Service.

fixing in F.A.A. (Johansen 1940). Slides were prepared using ordinary paraffin methods. Suberization in the dormant root tip was demonstrated with Sudan IV.

Observations

Soil moisture and soil temperature. Table 2 presents the figures of soil moisture and soil temperatures at 30 cm depth at the

TABLE 2. Soil temperatures and soil water content at a depth of 30 cm, from the sites of root sampling during the 1962/63 season. Soil temperatures in °C, soil moisture as percent by weight of dry soil.

Month	Rehovot		Panorama		Neve Ilan	
	Soil moist.	Soil temp.	Soil moist.	Soil temp.	Soil moist.	Soil temp.
Dec. 1962	9.6	--	22.4	15.0	32.8	13.0
Jan. 1963	2.6	18.0	13.7	18.3	19.7	17.2
Feb.	7.0	16.6	22.4	15.0	27.0	14.1
Mar.	4.7	15.3	19.0	13.2	32.1	12.5
Apr.	3.4	18.9	10 9	20.3	16.5	20.1
May	2.3	21.1	8.9	22.0	14.1	21.8
June	1.5	24.2	8.2	25.1	7.1	25.1
July	1.6	25.4	7.9	27.1	9.1	27.4
Aug.	1.4	26.2	7.3	27.5	10.4	27.6
Sept.	1.4	25.7	6.8	26.0	12.4	25.6
Oct.	1.5	25.7	7.8	25.9	13.7	24.0
Nov.	2.8	20.8	12.6	19.4	18.4	19.8

three selected sites during the survey period. The lowest soil temperature occurred at all localities in March with the absolute minimum of 12.5°, measured at Neve Ilan. Maximum soil temperature occurred at the end of August and the beginning of September, but did not exceed 27.6° (at Neve Ilan). It was found that soil moistures corresponding to 15 atm. were: at Rehovot 3.8 percent, at Panorama 16.5 percent, and at Neve Ilan 24.4 percent. Thus it is obvious that at all sites at a depth of 30 cm, the soil dries out far below the conventional wilting point during the summer months.

Organization of the dormant intermediary root. In the intermediary root of Aleppo pine, the cortex was composed of 6–8 layers or more or less isodiametric cells. At varying distances from the root apex the cells collapsed and the cortex turned brown, at first on the outside, and finally throughout. The death of the cortex, according to Aldrich-Blake (1930), is closely correlated with the attainment of the secondary condition in the endodermis, namely the total suberization of the cell walls. The dead brown cortex enveloped the stele for a long time and was not sloughed off before several divisions had taken place in the phellogen. Bleaching with NaC10 removed the brown coloration without disturbing the anatomical structure or destroying the suberin lamellas. The dormant root, brown throughout, appeared white after bleaching, except for a brown internal cap in

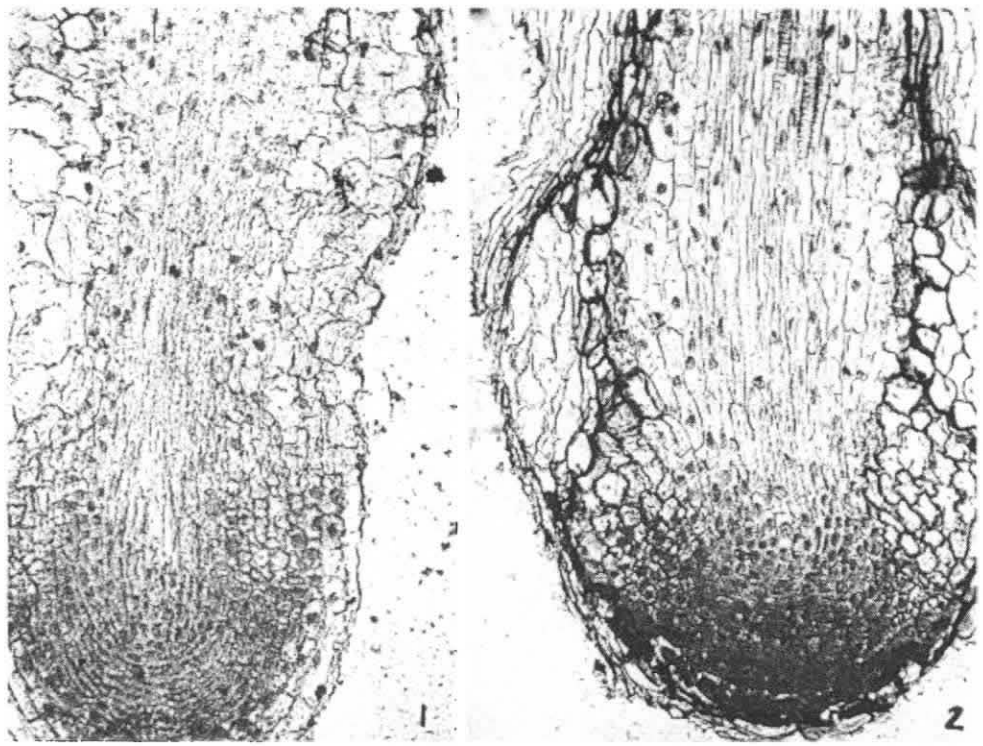

FIGURE 1. *Longitudinal section through an actively growing short root of Aleppo pine.* × *100.* FIGURE 2. *Longitudinal section through a dormant short root of Aleppo pine.* × *100. The sections were stained with Sudan IV. Note the cells with the dark walls which indicate the total suberization of the cells of the endodermis and the suberized layer which encloses the root tip. Above the whole layer the remnants of the former layer can be seen, which continue along the outer border of the new cortex.*

the root tip. This cap represents the metacutized layer, and crosswise brown bands the remnants of earlier isolating layers.

The brown cap and bands could also be bleached by treatment with NaCl O for 12 hours at 37°. The root cap of the longer roots was more developed and the brown cap was seen quite distinctly within, whereas in the shorter roots it was less developed and the metacutized layer was subterminal. Root hairs were poorly developed or completely absent. When present in the dormant root, they reached very close to the tip. They always arose out of cells of the second or third layer of the cortex.

A longitudinal section of the bleached root tip is shown in Figures 1 and 2. The metacutization was found to conform to type II of Plaut (1909). The secondary endodermis in the dormant root extended right up to the root apex. The suberized layer completely surrounded the initials and their immediate derivatives and by means of a cone frustum-like bridge across the cortex is united with the suberized cells of the secondary endodermis. Cap cells outside the metacutized layer collapsed and died, and therefore the layer became terminal. Vascular tissue differentiated much closer to the apical initials than in the actively growing root. The cells of the suberized layer as well as some of the cells adjoining it in the root cap, contained a dark brown substance. These cells formed the brown cap which is seen clearly with the naked eye in the dormant bleached root tips.

As growth of the dormant root was resumed, the suberized layer burst and a new root continued from the old one, with turgid cortex cells and a white root tip. The cortical bridge persisted and was seen in longitudinal sections as a brown band across the cortex, while the remnants of the layer which surrounded the apex were pushed to the outer boundary of the newly formed cortex. According to our observations an intermediary root of Aleppo pine may become dormant and resume growth several times. One can count from 2 to 6 brown cross bands on one bleached root, 1–3 cm in length. We could not determine whether they belonged to one or more annual growth cycles.

The periodicity of intermediary root dormancy. Bleaching of roots was found to be useful for easy classification of the root tips. A root tip with a brown cap was accepted as dormant while one without it was considered to be growing. Root tips collected every month at the three localities were classified as dormant or growing (Table 3).

At all three sites the number of growing root tips during winter and early spring differed considerably from those of the dry (summer) season. The ratio of growing to dormant root tips was especially high from December to March, dropping towards the middle of April and remaining low from May until August. At Rehovot this ratio was low even during the winter, but the overall pattern was similar to that of the other two localities. At Panorama there was a drop in January (which was unusually dry) but there was a steep rise in February and March.

A considerable rise in the ratio of growing to dormant root tips set in towards autumn, when we found a pronounced resumption of growth of dormant roots while new lateral roots appeared on long roots as well. At Rehovot and Panorama these phenomena were more pronounced than at Neve Ilan. New growth at the first two sites ceased at the end of September and began again in October with the renewal of rainfall. At Neve Ilan root growth activity began in the middle of August, ceased about the middle of September and was resumed towards the end of the month. Growth activity of feeder roots in late summer was reported by Kalela (1957) for Scotch pine, and ascribed by him to inner periodicity.

Phenological observations. Preliminary phenological observations were made on the same trees from which root samples

TABLE 3. Dormant or growing short root tips of Aleppo pine trees at three sites.

Month		Rehovot		Panorama		Neve Ilan	
		No. of root tips	Ratio of growing to dormant roots	No. of root tips	Ratio of growing to dormant roots	No. of root tips	Ratio of growing to dormant roots
Dec. '62	g[1]	--	--	97	3.7	43	3.6
	d	--		26		12	
Jan. '63	g	38	0.9	58	1.2	31	2.4
	d	42		47		13	
Feb.	g	46	1.6	131	1.8	8	1.3
	d	29		71		6	
Mar.	g	23	0.8	82	3.7	23	1.0
	d	29		22		23	
Apr.	g	23	0.7	74	0.3	15	1.1
	d	35		240		13	
May	g	7	0.2	19	0.1	2	0.2
	d	32		150		13	
June	g	14	0.2	19	0.2	10	0.3
	d	73		77		33	
July	g	5	0.2	14	0.08	4	0.4
	d	14		165		25	
Aug.	g	5	0.5	37	0.2	31	0.5
	d	11		240		69	
Sept.	g	30	0.9	62	0.9	13	0.3
	d	32		69		39	
Oct.	g	23	0.4	36	0.2	43	0.7
	d	58		182		60	
Nov.	g	37	1.3	64	1.4	68	0.8
	g	28		45		81	

[1] g—growing; d—dormant.

were taken. These observations were made mainly on branches of the lower portion of the leafy crown. They comprised opening of apical buds on the shoots in early spring, development and anthesis of male inflorescences, as well as the progress of growth of the young shoots and the brachyblasts following the shedding of the male inflorescences in April. The opening of the winter buds began in all stands in December or January; at the highest site, Neve Ilan, it started the earliest. Anthesis took place in March, continuing into April at Panorama. Growth of shoots and needles proceeded quickly in spring and diminished markedly in the dry summer months, especially in the mountain stands.

Discussion

Periodicity of root growth has been frequently discussed towards the end of the last century, and again in more recent times. According to Resa (1877) two main growing periods of the roots may be distinguished, the first from late winter until early spring and the second from late autumn until early winter. Büsgen (1901) concluded that the midsummer decline in root growth was a consequence of water stress and that low soil tempera-

ture was the main factor in stopping growth in winter. His conclusions were confirmed by many others (Hesselink 1926, Stevens 1931, Ladefoged 1939).

Although the results obtained from our observations vary to a considerable extent, they do permit some general conclusions. The main root growth takes place in winter, when the soil's water content is high and its temperature is not low enough to restrict growth. Growth ceases in the dry summer season. The same results were described by Cossmann (1939) for citrus roots.

This seems to confirm the conclusion that edaphic conditions are decisive in root growth. However, the data of Table 2 also show that in the annual activity at these three localities, there is neither a complete cessation of root growth nor general activity. During the periods of highest activity the percentage of growing roots reached only 70–80 percent, whereas in the dry season as much as 10–15 percent of the roots were found growing. According to Barney (1951) optimum growth rate of loblolly pine roots was at 25°. Thus, lack of general root activity in winter could, by principle, be due to low temperatures. However, root growth resumption and elongation occurred when soil temperature was far below Barney's optimum. Interesting enough, growth in the dry season occurred while soil moisture was decidedly below the conventional wilting point during the whole summer (see Table 2). It seems that resumption of growth does not depend only on edaphic conditions. It should be emphasized, however, that during the dry months the growth of the white root tips was very slow and lasted for only a short time.

The peak in root growth in late summer, which occurred even though there was no rainfall during that season is an additional indication that other factors are also inducing growth. Genetic factors may play a role in the occurrence of that apparently out-of-season growth. Wilcox (1962) attributes it to photoperiod. Cessation of growth is perhaps due to the severe water stress in the upper layers of the soil.

Our observations show that root growth cannot be predicted from shoot growth in winter or in summer. The main period of root growth lasted from November until mid-May. The onset of extensive root growth was not correlated with growth and developmental processes in the shoot. Bud opening began in March, i.e., much later than the start of root growth. Anthesis and general growth of shoots and needle fascicles took place from March to late August, i.e., when root growth began to be very restricted. A lack of correlation between root and shoot growth in conifers was recorded recently by Wilcox (1962); our results seem to corroborate the view of this author.

The concept of metacutization of the root tip not as an indication of senescence, but as producing a dormant structure from which renewed root growth can originate, was established by Plaut (1918), and since then was confirmed by some other authors (Aldrich-Blake 1930, Cossmann 1939, and Barney 1951). Plaut assumed that the low soil temperature in winter is a factor inducing metacutization of root tips. According to our observations, severe water stress is also a factor in that phenomenon. However, it should be emphasized that even under unfavorable conditions of soil drought we found roots growing.

According to Wilcox (1954, 1962) metacutization can originate during regular growth periods as well, when all exterior factors are at the optimum. Thus, perhaps metacutization is an anatomical phenomenon which occurs when the roots enter dormancy but is not necessarily connected directly with the factors inducing it. The results obtained indicate that, in spite of the obvious influence of endogenous factors in root growth, most roots will become dormant when external conditions are unfavorable, and will begin to grow when the conditions for it are favorable.

The fact that the brown cap and bands could also be bleached by a longer

treatment seems to indicate that the suberized cell walls of the metacutized layer interfere with the penetration of the bleaching liquid. Müller (1906) believed that suberization of root tips probably prevented the inward or outward passage of nutrients and also reduced the movement of water. Mager (1913) considered the dormant root cover as a protection from water loss liable to occur when the soil is frozen. Although water uptake through suberized cell walls was proven (Kramer 1946), the metacutized layer evidently protects the apex cells from early desiccation.

The main root activity of Aleppo pine starts with the onset of the rains, which usually occurs in November and continues through the spring. According to our studies, the period of shoot growth follows from early spring until midsummer. Oppenheimer (1945) has recorded cambial activity in trunks of Aleppo pines from February until November. Thus it seems that some growth activity continues throughout the year, indicating water resources at a considerable depth, from which the tree can draw even during the hot dry summer.

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